

The Anna's hummingbird chirps with its tail: a new mechanism of sonation in birds

Christopher James Clark* and Teresa J. Feo

Museum of Vertebrate Zoology, 3101 VLSB, University of California, Berkeley, Berkeley, CA 94720, USA

A diverse array of birds apparently make mechanical sounds (called sonations) with their feathers. Few studies have established that these sounds are non-vocal, and the mechanics of how these sounds are produced remains poorly studied. The loud, high-frequency *chirp* emitted by a male Anna's hummingbird (*Calypte anna*) during his display dive is a debated example. Production of the sound was originally attributed to the tail, but a more recent study argued that the sound is vocal. Here, we use high-speed video of diving birds, experimental manipulations on wild birds and laboratory experiments on individual feathers to show that the dive sound is made by tail feathers. High-speed video shows that fluttering of the trailing vane of the outermost tail feathers produces the sound. The mechanism is not a whistle, and we propose a flag model to explain the feather's fluttering and accompanying sound. The flag hypothesis predicts that subtle changes in feather shape will tune the frequency of sound produced by feathers. Many kinds of birds are reported to create aerodynamic sounds with their wings or tail, and this model may explain a wide diversity of non-vocal sounds produced by birds.

Keywords: hummingbird; sonation; tail feather; mechanical sound; display; *Calypte anna*

1. INTRODUCTION

Acoustic communication plays an important role in bird behaviour, sexual selection (Kroodsma & Byers 1991) and speciation (Price 1998). While the mechanisms of bird vocalizations have received considerable attention (Greenewalt 1968; Fletcher & Tarnopolsky 1999; Suthers *et al.* 1999), birds also produce a diversity of mechanical (non-vocal) sounds that are poorly described. Mechanical sounds are not created by the syrinx, but by other parts of the animal such as the wings or tail. They may be adventitious, produced incidentally and involuntarily as the part of another behaviour, or sonations (Bostwick & Prum 2003), in which the sound itself plays a role in communication. Some mechanical sounds are produced by physical contact between two structures, such as the percussive or stridulatory sounds made by the wings of manakins (Pipridae; Bostwick & Prum 2003, 2005). Other mechanical sounds are aerodynamic sounds produced by air flowing over or between a bird's feathers.

Aerodynamic sounds are created by air interacting with a solid object. Birds fly at high Reynolds numbers, so a large portion of the flow around them is turbulent. Turbulent flow produces sound (Fletcher 1992). Under most flow regimes, turbulence is random, causing random pressure fluctuations, resulting in atonal sounds characterized by a continuous distribution of sound frequencies. As a result, during flight, all birds, including owls (Kroeger *et al.* 1972), produce these atonal *whooshing* flight sounds.

In addition to these ubiquitous atonal sounds, many flying birds make tonal flight sounds, including swans (Carboneras 1992), guans (del Hoyo 1994), doves

(Mararchi & Baskett 1994), ducks (Lucas & Stettenheim 1972), snipes (Bahr 1907; Carr-Lewty 1943; Reddig 1978; Sutton 1981), hummingbirds (Aldrich 1938; Miller 1940; Rodgers 1940; Miller & Inouye 1983), nighthawks (Miller 1925; Cleere 1999), larks (Payne 1973; Bertram 1977) and honeyguides (Gill 2007). Many descriptions of tonal flight sounds call them whistles, but intend this as a description of the sound's tonality (Bostwick 2006), without specifying an underlying whistle mechanism.

Whistles are produced by purely aerodynamic mechanisms. Conventional whistles can be created by either air flowing through a constriction (Fletcher 1992), such as the sound produced by a tea kettle, or air flowing through a constriction and impinging on an edge (Fletcher 1992), as in a referee's whistle. Both of these mechanisms operate according to

$$f = St v/d \quad (1.1)$$

where f is the sound frequency; St is a constant (the Strouhal number); v is the air velocity; and d is a characteristic length particular to the specific kind of whistle (Fletcher 1992). In a third type of whistle, called an aeolian whistle, the turbulent wake behind a single object is not entirely random, and vortices form and are shed at a particular rate, creating a von Kármán vortex street (Fletcher 1992; Vogel 1994). Equation (1.1) still applies: d is the diameter of the object and the Strouhal number is approximately 0.2 (Fletcher 1992; Vogel 1994; White 1999). An example is the sound produced by telephone wires in high wind (Vogel 1994). According to these principles, if feathers whistle, it will either be due to air flowing through a gap between two feathers (a conventional whistle) or by one feather shedding vortices at a Strouhal number of approximately 0.2 (an aeolian whistle), and in either case, the sound frequency will be proportional to the air velocity.

* Author for correspondence (cclark@berkeley.edu).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2007.1619> or via <http://journals.royalsociety.org>.

Airflow can also produce tonal sounds if the air excites a solid to vibrate. Solids have resonant frequencies that are a function of their stiffness and shape (Blevins 1979). If moving air excites a feather, it may vibrate at or near its resonant frequency, producing a tonal sound. This is qualitatively similar to the reed in a wind instrument (Fletcher 1992; Fletcher & Rossing 1998). The solid's resonant frequency is not affected by air velocity, except by changes in the air's added mass (Blevins 1979; Vogel 1994; Argentina & Mahadevan 2005). Therefore, if feathers vibrate according to this mechanism, their frequency will vary little with air velocity.

Studies have used three kinds of evidence to show that a flight sound is mechanically produced by feathers, rather than vocally. First, the flight kinematics of many taxa suggest that their tonal flight sounds are non-vocal. For instance, the dive sound made by common nighthawks (*Chordeiles minor*) only occurs when the wings are turned down during a stereotypical dive, and this correlation between behaviour and sound production led Miller (1925) to conclude that the primary wing feathers create the dive sound. Second, experimental manipulations can show that particular feathers are necessary to produce a flight sound. Miller & Inouye (1983) demonstrated that gluing shut a gap between two wing feathers, eliminates the production of a 'wing whistle' emitted during flight of broad-tailed hummingbirds (*Selasphorus platycercus*). Third, laboratory experiments can demonstrate that particular feathers are sufficient to produce sounds similar to the flight sounds. For instance, isolated snipe tail feathers placed in moving air create sound similar to the 'drumming' noise produced during the species' characteristic dives (Bahr 1907; Carr-Lewy 1943; Reddig 1978).

In some cases, the origin of a flight sound is debatable (Bostwick 2006), such as a loud sound produced by male Anna's hummingbirds (*Calypte anna*). During a mating display, males ascend approximately 30 m in the air before dropping headfirst and swooping over a female (figure 1; Hamilton 1965; Stiles 1982). During the dive, a series of sounds are emitted (figure 2a). The loudest noise is called element C_{dive} (Baptista & Matsui 1979) and sounds like a brief loud *chirp* or *squeak*. It is tonal with a fundamental frequency of 4 kHz and higher harmonics, corresponding approximately to the musical note C_8 , four octaves above Middle C (figure 2a). Males have modified outer tail feathers, termed rectrix (R5; figure 3a,d). Rodgers (1940) reports that he 'attached an outer tail feather [R5] to a slender strip of bamboo. By whipping this through the air a note was produced, which was almost identical with that produced by the bird.' Baptista & Matsui (1979) were not convinced by Rodger's brief account, and observed that the Anna's hummingbird's song (figure 2b) has elements A_{song} , B_{song} and C_{song} that are spectrally and temporally similar to A_{dive} , B_{dive} and C_{dive} . They concluded that the dive sounds of the Anna's hummingbird are produced vocally. Stiles (1982; Stiles *et al.* 2005) disagrees, arguing that element C_{dive} seems louder than the song and too loud to be produced vocally.

Baptista & Matsui's (1979) results do not rule out the possibility that the tail produces element C_{dive} , and that acoustic similarity between the song and the dive sound has arisen via convergent evolution. Here, we show that element C_{dive} is a sonation created by fluttering of the trailing vane (T.V.) of the R5 tail feathers, using three lines

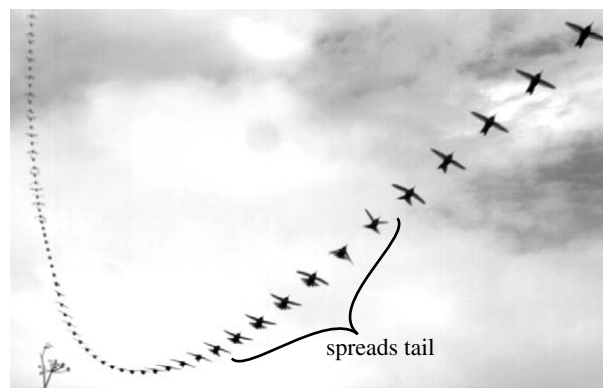


Figure 1. A composite image of a male Anna's hummingbird diving to a female, created using high-speed video. Consecutive images are 0.01 s apart. During the dive, males spread their tails for 0.06 s ($n=5$ videos) and simultaneously produce a loud sound (element C_{dive} in figure 2a) for 0.05 s ($n=53$ sound recordings). Videos of two dives are available in the electronic supplementary material.

of evidence: the kinematics of the dive; experiments on wild birds performing dives; and laboratory experiments on individual tail feathers.

2. MATERIAL AND METHODS

(a) Field experiments

Experiments on live Anna's hummingbirds were performed at the 'Albany Bulb' portion of the East Shore State Park, Albany, CA, in spring of 2006 and 2007.

Territorial male Anna's hummingbirds use a few (less than 10) stereotypical, conspicuous song perches. We located territorial males, and placed hummingbird feeders on their territories. Display dives were elicited from individual males by placing a stuffed mount of an Anna's hummingbird, or a live, caged hummingbird in a conspicuous location on a male's territory. A Sennheiser ME67 microphone was placed close to the cage or mount to record dives. Dive sound recordings were sampled at 48 kHz using a 16 bit digital recorder (Marantz PMD 670), and saved as uncompressed WAV files. Sound recordings were visualized using RAVEN v. 1.2.1 (Cornell Lab of Ornithology, Ithaca, NY; Charif *et al.* 2007) on a PC. Spectrograms were created using a Hann function with a 512 sample window.

Male Anna's hummingbirds dive in a vertical plane (the dive plane) oriented towards the Sun (Hamilton 1965), allowing us to anticipate the direction in which a bird would dive. We estimated dive speed by collecting video of 25 dives with digital camcorders (23 dives: 60 fps, 640×480 pixels with a Sony Handicam; 2 dives: 500 fps, 1280×1024 pixels with a Fastec Troubleshooter) placed approximately 20 m from and orthogonal to the dive plane. A metre stick was held horizontally and vertically in the camera's image plane, at the bottom of the display dive (where element C_{dive} is produced), as a calibration. Peak Motus (Vicon: Centennial, CO) was used to digitize the bird's position over time in the videos, and to calculate the bird's instantaneous velocity using a quintic spline. Accurate estimates of velocity depend on whether the bird's dive was really parallel to the image plane of the camera, and this method will underestimate the bird's true velocity if it was actually diving somewhat towards or away from the camera. Dives in which the bird's motion towards or away from the camera was small were used to calculate velocity, and none of our conclusions are affected by an underestimate of the bird's velocity.

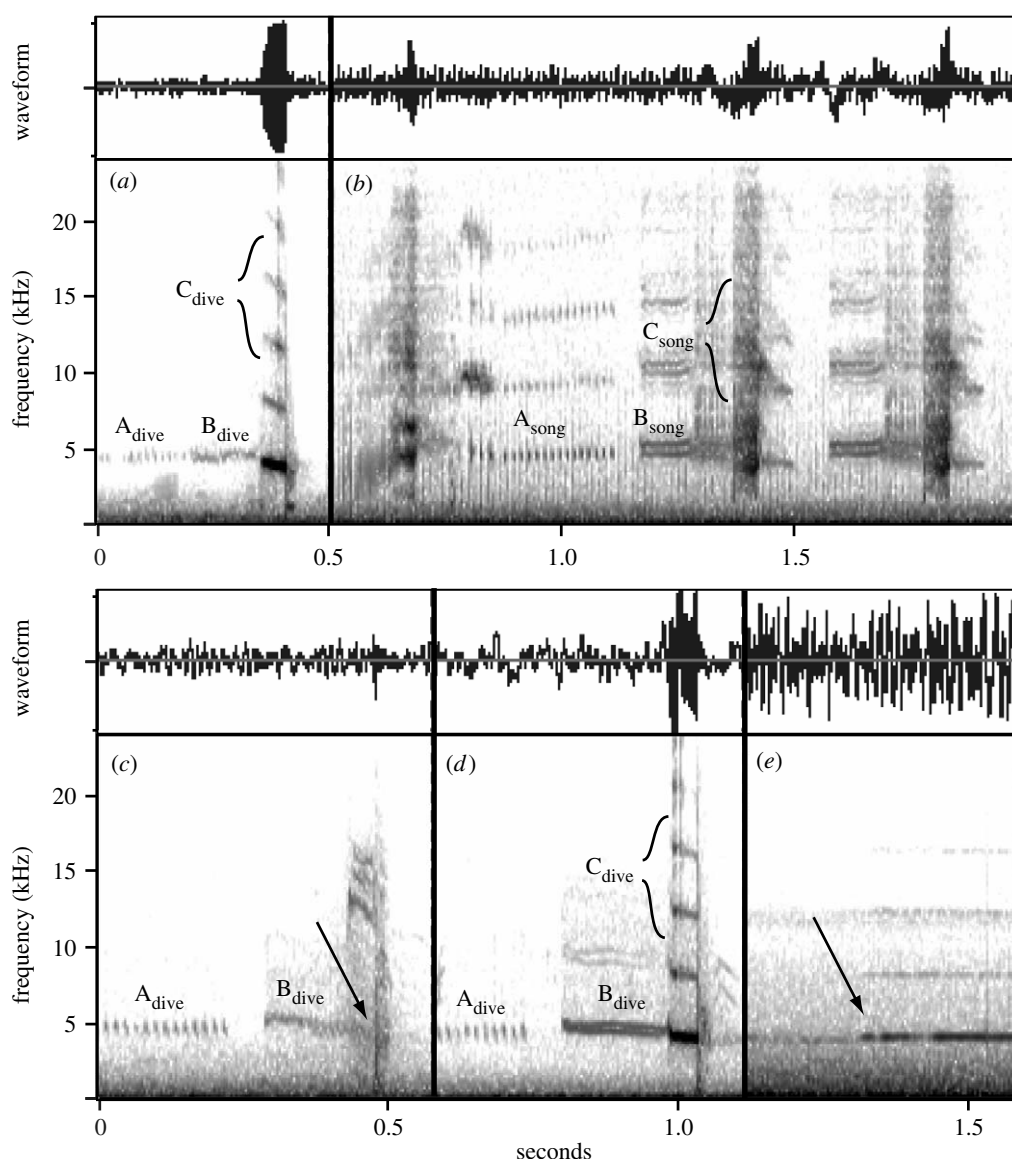


Figure 2. Spectrograms (showing frequency versus time) and waveforms (showing amplitude versus time) of sounds. Greyscale, relative sound energy, in which black indicates high sound energy, and white indicates low sound energy. All five sounds are from different recordings and therefore their waveforms cannot be directly compared due to different recording conditions. (a) Dive sound from an unmanipulated male, (b) song from a male hovering close to the microphone, (c) dive sound of a male with no trailing vane (T.V.), (d) dive sound of a male with no leading vane (L.V.) and (e) is the sound of an R5 feather producing sound in a wind tunnel at an airspeed of 26.2 m s^{-1} . A, B and C are the sound elements of the display dive or song, as defined by Baptista & Matsui (1979). With (a) unmanipulated birds and (d) birds missing the L.V. of R5, (b) C_{dive} is present with a fundamental frequency of 4 kHz, and is louder than the song. With birds missing the T.V. of R5 (c), C_{dive} is missing, and instead the bird produces a broad-spectrum 'whoosh' sound (indicated by the arrow). When R5 is placed in a wind tunnel (e), it produces a sound with a fundamental frequency of 4 kHz that matches a normal C_{dive} (initiation of sound production indicated by the arrow). The sound recordings used to create these spectrograms are available in the electronic supplementary material.

Five high-speed videos showing the tail kinematics of diving birds were also made with a Redlake Motion-Meter (Kodak; 500 fps, 292×210 pixels) or a Troubleshooter (Fastec; 500 fps, 1280×1024 pixels) camera. These videos were not synchronized with simultaneous sound recordings.

After pre-manipulation dives were recorded, we captured males using feeder traps, marked them with small spots of paint for identification and manipulated one bilateral pair of tail feathers. Two males had R5 plucked, two had the T.V. of R5 trimmed off, one had the leading vane (L.V.) of R5 trimmed off three males had R4 plucked and two males had R3 plucked. After manipulation, males were located on their territories, and post-manipulation dives were recorded within

two weeks of manipulation. Plucked feathers regrow in approximately five weeks.

Comparisons between the loudness of the song and display dive were obtained from three males. These males perched or hovered within 1 m of the microphone and sang, facing the microphone. Immediately prior to or following the song, they performed normal display dives, passing by at distances greater than 1 m from the microphone. In addition to differences in distance, two other factors introduce bias: in one instance the gain on the recorder was adjusted slightly in favour of the song seeming louder, and in the other two, the waveforms of the dive sounds exceeded the recorder's range of sensitivity. All three factors bias the songs to seem louder, whereas our hypothesis is that the dive sound is louder (Stiles 1982).

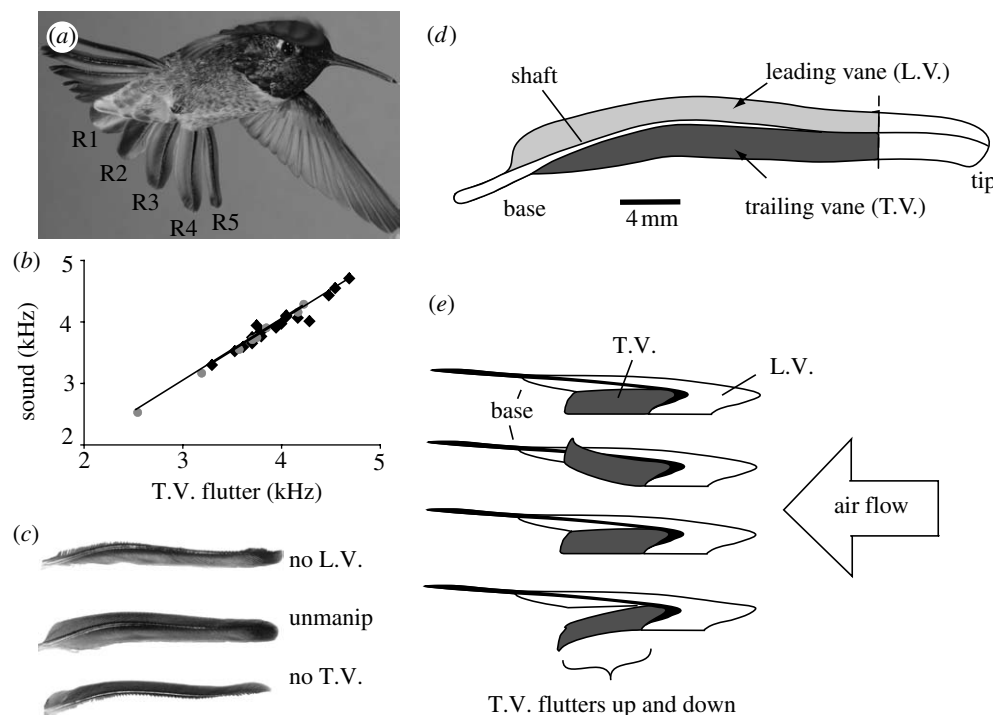


Figure 3. A description of the fluttering of the trailing vane (T.V.) of R5. (a) A male Anna's hummingbird with tail feathers (rectrices) labelled as R1 through R5. (b) Frequency of the T.V. flutter and that of sound (f) are highly correlated (linear regression, unmanipulated feathers: slope = 0.996, $r^2 = 0.94$, $p < 0.0001$, $n = 18$); circles, feathers missing L.V.; diamonds, unmanipulated feathers. The correlation between sound production and the T.V. flutter is unaffected by removing the leading vane (L.V.) of the feather (linear regression, feathers lacking L.V.: slope = 1.00, $r^2 = 0.98$, $p < 0.0001$, $n = 8$). (c) Photos of an unmanipulated R5, R5 with the L.V. removed and R5 with the T.V. removed. (d) An outline of the R5 showing the base, tip, shaft, L.V. and T.V.. (e) Four end-on views showing the up-and-down fluttering motion of the T.V. (in grey), relative to the direction of airflow. The tip of the feather is not shown in this perspective. Two videos showing the feather fluttering are available in the electronic supplementary material.

(b) Laboratory experiments

Tail feathers were collected from wild adult Anna's hummingbirds caught in Berkeley, CA. We produced sounds using just the feathers with two methods: by placing them in front of a jet of air, or by putting them in a wind tunnel.

(i) Jet experiments

Tones were produced by placing the male R5 tail feathers approximately 2 cm in front of a jet of air issued from a hose. The outer or L.V. of the feather faced into the jet, and the angle of attack of the feather was nominally 0° (ignoring aeroelastic deformation of the feather, which was estimated by eye to be less than 10° along the entire feather). A Sennheiser ME 67 shotgun microphone was placed next to the jet to record sound, using the same equipment and settings as the field experiments. The feather was illuminated using two halogen lights, and video was collected at 20 000 fps (Photron Fastcam APX RS, resolution: 512×256 pixels). Sound and video recordings were manually synchronized to the nearest 1 s.

The jet was made of two lengths of Nalgene premium tubing (5/16 in. i.d.) each connected to a pressurized air source. Seven straws (3 mm diameter) were inserted 13 cm deep into the end of each tube to make the flow more laminar. This improved the consistency of sounds produced by the feathers. The ends of the tubes were placed side-by-side to make a jet that was 2 by 1 cm in cross section. It was large enough to contain the majority, but not all, of a feather within the airflow. The use of jets with larger cross-sectional area (that would contain more of the feather within the airflow) was not possible due to the higher levels of background noise produced by them. The speed of the jet was measured with a Kurtz 2440

thermal anemometer 2 cm from the jet (in the same location as the feather), and was on average 40 m s^{-1} . It is not clear whether the turbulence of the jet affected the anemometer's accuracy. The value of 40 m s^{-1} was used solely to ensure similar aerodynamic conditions across all experiments that used the jet, at a velocity well above the feather's critical velocity. The airflow did not represent aerodynamic conditions identical to those the feathers experience during a dive, but tones produced in front of the jet under these conditions matched the frequencies of sounds produced by feathers placed in a wind tunnel (see below).

We performed two experimental manipulations: (i) cutting off the T.V. of the feather ($n = 3$ feathers) or (ii) cutting off the L.V. of the feather ($n = 3$ feathers). To assess changes caused by experimental manipulations, we placed feathers in the jet of air perpendicular to airflow, and adjusted their orientation slightly (if necessary) until they produced sound. Most unmanipulated male R5 feathers begin producing sounds immediately when placed in the jet, and if for some reason a feather did not initially produce sound, manipulating its orientation for less than 10 s was sufficient to produce a tone.

If an experimentally manipulated feather did not produce a sound after at least 1 min of adjusting its orientation, it was scored as not producing sound. Simultaneous sound recordings and high-speed video (20 000 fps) were taken for each feather, and it was then removed from the jet. Each feather was measured three times before manipulation, and three times after manipulation. We calculated the frequency of the fluttering motion of the feather by counting the number of frames necessary for 15 cycles of oscillation.

Table 1. Results of experimental manipulation of feathers R3, R4 and R5 on wild Anna's hummingbirds. (Italics indicate manipulations that resulted in a statistically significant change in the proportion of dives with element C present (χ^2 -tests, $p < 0.002$).)

feather manipulation	proportion of pre-manipulation dives with element C present	result of manipulation	N (birds)
pluck R5	100% ($n=20$ dives)	<i>element C eliminated (present in 0 of 37 dives)</i>	2
remove trailing vane of R5	100% ($n=67$ dives)	<i>element C eliminated (present in 0 of 87 dives)</i>	2
remove leading vane of R5	100% ($n=9$ dives)	no difference (13 of 14 dives with element C)	1
pluck R4	100% ($n=13$ dives)	<i>can still produce element C (9 of 18 dives with element C)</i>	3
pluck R3	97.5% ($n=39$ dives)	no difference (14 of 14 dives with element C)	2

(ii) Wind tunnel experiments

We placed feathers in a high-speed wind tunnel at the John Hopkins Marine Research Station, Stanford University, CA. Feathers were attached to a beam projecting into the working section of the tunnel, along with a TSI VelociCalc thermal anemometer placed just upstream and above the feather to measure the air velocity. Rotating the beam allowed the angle of attack of the feather to be changed, and the base of the feather was always perpendicular to the airflow. Audio recordings were taken with a Sennheiser ME 67 microphone attached to the outside of the tunnel near the feather. Placing the microphone inside the tunnel was not possible due to noise caused by turbulence, and because the microphone's windshield blocked roughly 10% of the cross section of the working section, causing noticeable changes to the tunnel's velocity. Attached to the outside of the tunnel, the microphone was approximately 20 cm from the feather, with an acrylic barrier (the wall of the working section of the wind tunnel) between the two. Also, the tunnel motor produced extremely high levels of background noise. Despite these constraints, the male R5 produced loud sounds clearly audible to us outside the wind tunnel, and unambiguously recorded by the microphone (figure 2e).

The wind tunnel was first set to 26.2 m s^{-1} and then wind speed was decreased in increments of 1.6 m s^{-1} until the feather ceased producing sound. The presence or absence of sound production was determined by ear, as, given the constraints of our setup, the microphone was not more sensitive than our own hearing. Once the feather stopped producing sound, the wind velocity was increased in increments of 0.7 m s^{-1} until the feather once again began to produce a tone. At each speed, we slowly rotated the angle of attack of the feather from -90° to 90° ; the tone's frequency varied little with the angle of the attack, and the feather was rotated to ensure that it did or did not make sound regardless of its orientation. A feather's critical velocity was defined as the minimum velocity at which it produced audible sound.

3. RESULTS

The high-speed video (500 fps) of males performing display dives revealed that they began the dive with their tail shut, then abruptly spread their tail at the bottom of the dive and held it open for an average of $0.059 \pm 0.007 \text{ s}$ (figure 1; $n \pm \text{s.d.}$; $n=5$). Males spread their tails at the same time element C_{dive} was produced at the bottom of the dive. Sound recordings of display dives indicated that element C_{dive} lasted for $0.052 \pm 0.006 \text{ s}$ ($n \pm \text{s.d.}$; $n=53$). In unmanipulated males, the sound measurements indicated that element C_{dive} had a fundamental frequency

of $4.1 \pm 0.2 \text{ kHz}$ with harmonics ($n=53$; figure 2a); however the birds travelled $23.1 \pm 3.1 \text{ m s}^{-1}$ ($n \pm \text{s.d.}$ $n=25$) at the bottom of the dive, causing further uncertainty in the sound's true frequency due to a Doppler shift of up to $\pm 0.3 \text{ kHz}$. Element C_{dive} was at least 18 dB louder than any part of the song (paired t -test, $p=0.0005$, d.f.=2). This was despite three variables (microphone distance, recorder gain and the recorder's limited range of sensitivity) that would bias the song to make it seem relatively louder (figure 2a,b). Two videos of dives are available in the electronic supplementary material.

The results of experiments on wild males are summarized in table 1. Experimental manipulation showed that the T.V. of the R5 tail feathers must be present for the birds to produce the dive sound. Unmanipulated males produced element C_{dive} in 97.3% of dives ($n=402$ dives across 24 birds). All males with R3 or R4 removed produced element C_{dive} in at least one of their display dives. Likewise, a male with the L.V. of R5 removed also produced element C_{dive} in most of his dives (figure 2d). However, males that had their entire R5 removed, or the T.V. of R5 removed (figure 3c), never produced element C_{dive} after manipulation (table 1; figure 2c). Some sound is still produced (see vicinity of arrow in figure 2c), but it is a broad-spectrum sound and generally atonal. Sound files used to make figure 2 are available in the electronic supplementary material.

Isolated male R5 feathers made tonal sounds at the same frequency as element C_{dive}. Unmanipulated R5 produced tones with fundamental frequencies ranging from 3.3 to 4.7 kHz, with harmonics, in front of a jet of air (figure 3b) or in a wind tunnel (figure 2e). R5 feathers with the L.V. removed (figure 3c) also produced sounds with frequencies ranging from 2.5 to 4.5 kHz ($n=3$ feathers). However, R5 did not produce sounds after the T.V. was removed ($n=3$ feathers). Male R4 and R3 feathers also made sounds in a jet of air, at frequencies below 2.5 kHz. Additionally, male R5 feathers made a second sound that is associated with the feather's tip, but at a frequency below 1.5 kHz.

The high-speed video (20 000 fps) of feathers placed in the jet revealed that while a feather made a tone, the T.V. of the feather fluttered at the same frequency as the sound (figure 3b) while the shaft and L.V. were immobile (figure 3e). The T.V. of the feather is a sheet of connected barbs with one edge anchored to the shaft, and free at the opposite edge (the trailing edge). When the feather produced sound, the trailing edge of the sheet fluttered up and down. In most videos, a travelling wave appeared to move down the feather, either from base to tip or from

tip to base (see videos in the electronic supplementary material). Sometimes this travelling wave was absent, but the feather still fluttered and produced the 4 kHz sound. When the barbs were separated from each other so that they no longer formed a continuous sheet, the T.V. no longer fluttered in synchrony, and no sound was detected above the background noise of the jet. Manually reconnecting the barbs to reform the sheet enabled the feather to once again produce audible sound. The frequency of the sound was almost perfectly correlated with the frequency of the flutter (regression, slope = 0.996, $r^2 = 0.94$, $p < 0.0001$, $n = 18$; figure 3b). Two high-speed videos of feathers fluttering in the jet are available in the electronic supplementary material.

When R5 feathers were placed in a wind tunnel, the frequency (f , kHz) of the sound was positively correlated with air velocity (v , m s^{-1}): ($f = 0.056 \times v + 2.6$, linear regression, slope $p < 0.001$, intercept: $p < 0.001$, $n = 34$ samples, figure 4). Below a critical minimum velocity of $19.6 \pm 1.1 \text{ m s}^{-1}$ ($n \pm \text{s.d.}$, $n = 6$ birds), the feathers stopped making audible sounds.

4. DISCUSSION

The high-speed video indicates that the Anna's hummingbird spreads its tail at the bottom of the display dive (figure 1). Element C_{dive} lasts for the same amount of time as the tail is spread, and occurs at the same part of the dive. This suggests that spreading the tail plays a role in the production of the 4 kHz dive sound. Removing R5 or trimming the T.V. of R5 eliminates element C_{dive} of the dive sound in wild birds (figure 2c). These manipulated birds still produce an atonal sound (figure 2c), but we hypothesize that this is an adventitious sound made by turbulent airflow over the body, wings and tail of the bird as it flies by the microphone. Males with no R3, R4 or a L.V. of R5 could still generate element C_{dive} (figure 2d). When placed in a jet of air, or in a wind tunnel, the T.V. of R5 flutters and can produce a 4 kHz sound, at the velocities reached by male when element C_{dive} is produced during a dive (figure 4). Therefore, the T.V. of R5 is both necessary and sufficient to produce element C_{dive} . We conclude that element C_{dive} is a sonation produced by the fluttering of the T.V. of the R5 tail feathers.

(a) Acoustic mechanisms

Our data suggest that the mechanism generating element C_{dive} is not a whistle. First, morphology rules out the conventional whistle hypothesis. Conventional whistles require a gap for air to flow over or through, which would be created by two feathers or possibly a gap in the barbs of one feather. Although plucking the R4 feather did significantly decrease the fraction of dives with element C_{dive} present (table 1), suggesting R4 does play a role in sound production, all three manipulated birds produced element C_{dive} at least once when missing their R4s (table 1), and R5 alone can generate the sound in a wind tunnel, with no gap present. Thus, the sound is not a conventional whistle. The C_{dive} is also not an aeolian whistle or tone, with tonality produced by vortex shedding (Fletcher 1992), for four reasons. First, given a Strouhal number of 0.2 (Vogel 1994; White 1999), a feather width of 4 mm (figure 3d) and a velocity of 23 m s^{-1} at the bottom of the dive (figure 4), this hypothesis predicts a

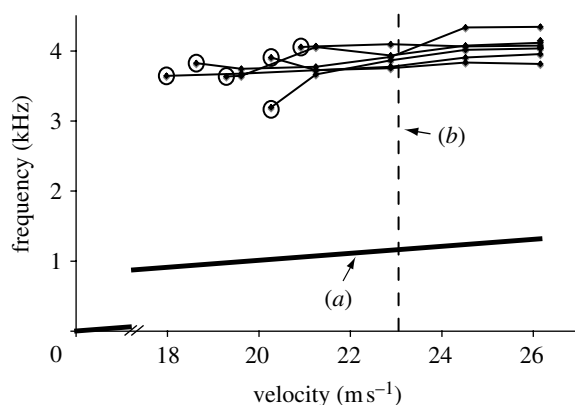


Figure 4. Frequency of sound produced by six male R5 feathers over a range of air velocities in a wind tunnel. Frequency (f , kHz) is positively correlated with velocity (v , m s^{-1}): $f = 0.056 \times v + 2.6$ (linear regression, slope: $p < 0.001$, intercept: $p < 0.001$, $n = 34$ samples). The minimum velocity at which each feather would produce sound is circled. (a) The predicted sound frequency for the aeolian whistle hypothesis, according to equation (1.1), and assuming $St = 0.2$ and $d = 4 \text{ mm}$. (b) The birds travel an average of 23.1 m s^{-1} at the bottom of the dive, which is greater than the average critical velocity of 19.6 m s^{-1} .

frequency of 1 kHz, not 4 kHz. Second, none of the whistle hypotheses predict a critical velocity for sound production, but all of the R5 tail feathers ceased producing sound at around the same air velocity. Third, although frequency and velocity are positively correlated (figure 4), the slope is one-third of that predicted by equation (1.1). Moreover, the whistle hypothesis predicts that the y -axis intercept should be near zero, rather than the value of 2.6 kHz extrapolated from the regression (figure 4). Fourth, according to the whistle hypothesis, experimental manipulations of the T.V. should change the tone of the sound (by changing d from equation (1.1)), but not necessarily eliminate sound production. Instead, manipulations of the T.V. eliminated the feather's ability to produce sound.

Our data are consistent with the flag hypothesis, in which the sound is produced by the feather fluttering at its resonant frequency. The experiments indicate the T.V. of the R5 as the source of the sound, suggesting that the resonance lies within the mechanical properties of the T.V. of the feather. Reeds in wind instruments (Fletcher & Rossing 1998) and flags (Argentina & Mahadevan 2005) represent two structures that vibrate in fluid flow at a resonant frequency determined by their elastic modulus and shape. Argentina & Mahadevan (2005) derive equations predicting that a flag flutters when the airflow exceeds a critical velocity, and that above this velocity the flutter frequency is insensitive to wind velocity. The R5 feathers have a critical minimum velocity for sound production and therefore a critical velocity for fluttering (figure 4). Above the critical velocity, the frequency produced by R5 changes little with wind velocity (figure 4). Both of these results are consistent with Argentina & Mahadevan's (2005) model, therefore we fail to reject the flag model as the mechanism of sound production.

(b) Evolutionary implications

According to the flag model, a feather's shape and material properties (i.e. elastic modulus of β -keratin) together set its pitch, which changes little over a range of air velocities.

Evolution could theoretically change either shape or elastic modulus to alter the tone produced by a feather. However, feather keratin appears to have an invariant elastic modulus across diverse avian taxa (Bonser & Purslow 1995), suggesting that flight sounds are not tuned by modifying this variable. By contrast, feather shape is determined by variation in barb length, barb diameter and barbule morphology, which are evolutionarily labile traits (Prum & Williamson 2001). Therefore, this seems the simplest pathway for evolution to modify the frequency of flight sounds produced by feathers. According to this hypothesis, aspects of feather shape should correlate highly with the sounds produced by feathers.

A second prediction of the flag model is that feather tones are only created when airflow over the feather exceeds a critical velocity. This suggests that tonal flight sounds will only be associated with behaviours that produce rapid airflow over the feathers. For sounds produced by primary wing feathers, birds could attain sufficient local air velocities to produce sound by varying their wing-beat kinematics. Mourning doves (*Zenaidura macroura*) make a tonal sound that appears to be mechanically produced by the wings (Mararchi & Baskett 1994). This sound is produced primarily during take-off, which may be due to the high wingtip velocity caused by take-off kinematics. For other feathers, such as tail feathers, varying flight speed is the main option available to modulate local air velocity in order to exceed a feather's critical velocity. The Anna's hummingbird is a case in point: the behaviour of diving appears necessary to reach the critical velocity to create element C. The R5's critical velocity of $19.6 \pm 1.1 \text{ m s}^{-1}$ (figure 4) is faster than the top speed of 13 m s^{-1} at which the birds were observed to fly in the wild (Stiles 1982), or the top speed of $15.1 \pm 0.48 \text{ m s}^{-1}$ ($n=15$) at which males are capable of flying in a wind tunnel (Clark & Dudley in preparation). Many other species of bird, such as snipes, nighthawks and other hummingbirds, also perform dive displays while producing putative sonations. This suggests that diving from a height may be a common strategy for achieving velocities high enough to reach the feather's critical velocity.

The Anna's hummingbird can sing at the same frequency as the dive sounds (figure 2a,b), raising the question of why it has evolved a second mode of sound production. The Anna's hummingbird's sister species, the Costa's hummingbird (*Calypte costae*; McGuire *et al.* 2007), also reportedly sings and produces its dive sounds vocally, and these sounds are acoustically similar (Wells *et al.* 1978). Its unusually shaped R5s are approximately 2 mm in width (the Anna's is 4 mm), and the flag hypothesis predicts that smaller widths will produce higher-frequency sounds. The Costa's dive sound has higher frequency than the Anna's dive sounds (Wells *et al.* 1978). These patterns suggest that the Costa's dive sound could be produced by the tail as well. If true, the convergence in song and dive sounds may not be unique to the Anna's hummingbird, indicating that selection favours similar acoustic features in both types of acoustic signals. While sexual selection seems to be the most likely cause of this convergence, the dive's function is unclear. Males perform dive to females, other males, other species of birds and even to humans (Stiles 1982; but see Hurley *et al.* 2001).

Non-vocal mechanisms, such as this tail feather sonation, enhance the diversity of sounds birds can produce. Small birds may be limited in their ability to produce loud vocal sounds by the size of their syrinx (Brackenbury 1979). The dive sound of the Anna's hummingbird is much louder than its song (figure 2a,b). This suggests that switching to feather sonations has allowed it to escape the intrinsic constraints on vocal sound volume. In the bee hummingbird clade (which includes the Anna's hummingbird), many related species perform dives (Banks & Johnson 1961; Stiles 1983; Clark 2006), have species-specific tail morphologies (Banks & Johnson 1961; Wells *et al.* 1978) and make a diverse array of sounds (Wells *et al.* 1978). This is likewise true for snipes (Bahr 1907; Sutton 1981). We predict that in these clades, dive behaviours and tail morphology have coevolved to produce a diversity of mechanical sounds.

All procedures were approved by the UC Berkeley Animal Care and Use Committee and performed under the relevant government permits to film, capture and band hummingbirds.

We are indebted to M. Koehl, B. Full, R. Dudley, M. Denny and especially S. Patek for use of equipment; to N. Reeder, J. Derbridge, A. Haiman, S. Weinstein, A. Shultz, G. Byrnes, A. Varma and S. van Duin for assistance in the field; to S. Patek, L. Mahadevan, N. Fletcher, S. Sane, M. deVries, J. McGuire, the Dudley laboratory and members of the MVZ for advice and discussion; and to the USFWS, CA Department of Fish and Game, Patuxent Bird Banding Lab, California State Parks and East Bay Regional Parks for research and filming permits. Funding was provided by the Museum of Vertebrate Zoology, and R. Dudley. C.J.C. performed the field experiments and wrote the majority of the paper as a part of a PhD thesis. T.J.F. designed and performed the laboratory experiments as an undergraduate honours thesis, and contributed substantially to fieldwork, data analysis and writing.

REFERENCES

- Aldrich, E. C. 1938 Natural history of the Allen hummingbird (*Selasphorus aleni*). Unpublished M.A. thesis, UC Berkeley.
- Argentina, M. & Mahadevan, L. 2005 Fluid-flow-induced flutter of a flag. *Proc. Natl Acad. Sci. USA* **102**, 1829–1834. (doi:10.1073/pnas.0408383102)
- Bahr, P. H. 1907 On the "bleating" or "drumming" of the snipe (*Gallinago coelestis*). *Proc. Zool. Soc. Lond.* (Pt 1), 12–35.
- Banks, R. C. & Johnson, N. K. 1961 A review of North American hybrid hummingbirds. *Condor* **63**, 3–28. (doi:10.2307/1365419)
- Baptista, L. F. & Matsui, M. 1979 The source of the dive-noise of the Anna's hummingbird. *Condor* **81**, 87–89. (doi:10.2307/1367863)
- Bertram, B. C. R. 1977 Variation in the wing-song of the flappet lark. *Anim. Behav.* **25**, 165–170. (doi:10.1016/0003-3472(77)90079-3)
- Blevins, R. D. 1979 *Formulas for natural frequency and mode shape*. New York, NY: Van Nostrand Reinhold Company.
- Bonser, R. H. C. & Purslow, P. P. 1995 The Young's modulus of feather keratin. *J. Exp. Biol.* **198**, 1029–1033.
- Bostwick, K. S. 2006 Mechanisms of feather sonation in Aves: unanticipated levels of diversity. *Acta Zool. Sin.* **52S**, 68–71.
- Bostwick, K. S. & Prum, R. O. 2003 High-speed video analysis of wing-snapping in two manakin clades (Pipridae: Aves). *J. Exp. Biol.* **206**, 3693–3706. (doi:10.1242/jeb.00598)

- Bostwick, K. S. & Prum, R. O. 2005 Courting bird sings with stridulating wing feathers. *Science* **309**, 736. (doi:10.1126/science.1111701)
- Brackenbury, J. H. 1979 Power capabilities of the avian sound-producing system. *J. Exp. Biol.* **78**, 163–166.
- Carboneras, C. 1992 In *Handbook of the birds of the world*, vol. 1 (eds J. del Hoyo, A. Elliott & J. Sargatal). Ostrich to ducks, Barcelona, Spain: Lynx Edicions.
- Carr-Lewty, R. A. 1943 The aerodynamics of the drumming of the common snipe. *Br. Birds* **36**, 230–234.
- Charif, R. A., Clark, C. W. & Fristrup, K. M. 2007 *RAVEN PRO 1.3 user's manual*. Ithaca, NY: Cornell Laboratory of Ornithology.
- Clark, C. J. 2006 Observations on the vervain hummingbird's (*Mellisuga minima*) display dive and territorial behavior. *Ornithol. Neo.* **17**, 403–408.
- Clark, C. J. & Dudley, R. In preparation. Tail elongation comprises fast forward flight of humming birds.
- Cleere, N. 1999 Family Caprimulgidae (nightjars). In *Handbook of the birds of the world*, vol. 5 (eds J. del Hoyo, A. Elliott & J. Sargatal). Barn-owls to hummingbirds, Barcelona, Spain: Lynx Edicions.
- del Hoyo, J. 1994 Family Cracidae (chachalacas, guans and curassows). In *Handbook of the birds of the world*, vol. 2 (eds J. del Hoyo, A. Elliott & J. Sargatal). New World vultures to guineafowl. Barcelona, Spain: Lynx Edicions.
- Fletcher, N. H. 1992 *Acoustic systems in biology*. New York, NY: Oxford University Press.
- Fletcher, N. H. & Rossing, T. D. 1998 *The physics of musical instruments*. New York, NY: Springer.
- Fletcher, N. H. & Tarnopolsky, A. 1999 Acoustics of the avian vocal tract. *J. Acoust. Soc. Am.* **105**, 35–49. (doi:10.1121/1.424620)
- Gill, F. B. 2007 *Ornithology*. New York, NY: Freeman and Company.
- Greenewalt, C. H. 1968 *Bird song: acoustics and physiology*. Washington, DC: Smithsonian Institution Press.
- Hamilton III, W. J. 1965 Sun-oriented display of the Anna's hummingbird. *Wils. Bull.* **77**, 38–44.
- Hurly, T. A., Scott, R. D. & Healy, S. D. 2001 The function of displays of male rufous hummingbirds. *Condor* **103**, 647–651. (doi:10.1650/0010-5422(2001)103[0647:TFO-DOM]2.0.CO;2)
- Kroeger, R. A. et al. 1972 *Low speed aerodynamics for ultra-quiet flight*. Technical Report AFFDL TR 71–75, pp. 1–155. Air Force Flight Dynamics Lab, Wright-Patterson Air Force Base, Ohio.
- Kroodsma, D. E. & Byers, B. E. 1991 The function(s) of bird song. *Am. Zool.* **31**, 318–328.
- Lucas, A. M. & Stettenheim, P. R. 1972 *Avian anatomy: integument part 1*. Washington, DC: US Department of Agriculture.
- Mararchi, R. E. & Baskett, T. S. 1994 *Mourning dove (Zenaida macroura)*. The birds of North America. Philadelphia, PA: The Academy of Natural Sciences.
- McGuire, J., Witt, C. C., Altshuler, D. L. & Remsen, J. V. J. 2007 Phylogenetic systematics and biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. *Syst. Biol.* **56**, 837–856. (doi:10.1080/10635150701656360)
- Miller, A. H. 1925 The boom-flight of the Pacific nighthawk. *Condor* **27**, 141–143. (doi:10.2307/1362990)
- Miller, L. 1940 Sound produced in the nuptial dive of young Anna hummingbirds. *Condor* **42**, 305–306.
- Miller, S. J. & Inouye, D. W. 1983 Roles of the wing whistle in the territorial behavior of male broad-tailed hummingbirds (*Selasphorus platycercus*). *Anim. Behav.* **31**, 689–700. (doi:10.1016/S0003-3472(83)80224-3)
- Payne, R. B. 1973 Wingflap dialects in the flappet lark *Mirafra rufocinnamomea*. *Ibis* **115**, 270–274.
- Price, T. 1998 Sexual selection and natural selection in bird speciation. *Phil. Trans. R. Soc. B* **353**, 251–260. (doi:10.1098/rstb.1998.0207)
- Prum, R. O. & Williamson, S. 2001 Theory of the growth and evolution of feather shape. *J. Exp. Zool.* **291**, 30–57. (doi:10.1002/jez.4)
- Reddig, v. E. 1978 Der Ausdrucksflug der Bekassine (*Capella gallinago gallinago*). *J. Ornithol.* **119**, 357–387. (doi:10.1007/BF01643130)
- Rodgers, T. L. 1940 The dive note of the Anna hummingbird. *Condor* **42**, 86. (doi:10.2307/1363949)
- Stiles, F. G. 1982 Aggressive and courtship displays of the male Anna's hummingbird. *Condor* **84**, 208–225. (doi:10.2307/1367674)
- Stiles, F. G. 1983 Systematics of the southern form of *Selasphorus* (Trochilidae). *Auk* **100**, 311–325.
- Stiles, F. G., Altshuler, D. L. & Dudley, R. 2005 Wing morphology and flight behavior of some North American hummingbird species. *Auk* **122**, 872–886. (doi:10.1642/0004-8038(2005)122[0872:WMAFBO]2.0.CO;2)
- Suthers, R. A., Goller, F. & Pytte, C. L. 1999 The neuromuscular control of birdsong. *Phil. Trans. R. Soc. B* **354**, 927–939. (doi:10.1098/rstb.1999.0444)
- Sutton, G. M. 1981 On aerial and ground displays of the world's snipes. *Wils. Bull.* **93**, 457–477.
- Vogel, S. 1994 *Life in moving fluids*. Princeton, NJ: Princeton University Press.
- Wells, S., Bradley, R. & Baptista, L. F. 1978 Hybridization in *Calypte* hummingbirds. *Auk* **95**, 537–549.
- White, F. M. 1999 *Fluid mechanics*. New York, NY: McGraw-Hill.